

THE ACOUSTICAL BEHAVIOR OF SOME FISHES IN THE BIMINI AREA ^{1, 2}

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While many kinds of marine organisms are recognized as sound sources, it is not clear in most cases under what conditions the species concerned became sonic in nature, nor what patterns of behavior the sounds normally accompany. Spontaneous sound production, by many fishes known to produce sounds, tends to become partially or completely suppressed in captivity (Dobrin, 1947; Fish, 1948; Moulton, 1956b); one must frequently resort to artificial stimuli such as handling or electric shock (Fish, 1954; Fish *et al.*, 1952) to elicit any sound for study. Failure of free fishes to respond consistently to man-made sounds introduced into the water (Moulton and Backus, 1955) has aroused considerable interest, evident in writings since the time of Aristotle, in the role that the sounds of fishes themselves play in nature.

In order to obtain further information on the production of fish sounds and their significance to fish behavior, the period from 13 June to 13 August 1956 was spent at the Lerner Marine Laboratory of the American Museum of Natural History on North Bimini, Bahama Islands. A glass-panelled power boat and the clarity of the water facilitated extensive observation of near-shore fishes during underwater listening, and well-stocked fish pens provided opportunity for close observation of such fishes in a reasonably natural environment. Recordings of marine sounds, accompanied by notes on simultaneous observations, have been compared with recordings made in the laboratory from carefully identified specimens. The identity of certain sounds recorded at sea and in the laboratory has been determined by this aural comparison and by the study of vibrograms made at the Woods Hole Oceanographic Institution.

The fishes most frequently heard along the western edge of the Great Bahama Bank in the Bimini area, the Nassau grouper, *Epinephalus striatus* (Bloch), and the squirrelfish, *Holocentrus ascensionis* (Osbeck), are inhabitants of relatively shallow water. That sightings of the Nassau grouper and squirrelfish occurred only in areas where incidence of their calling was high, and that these species were generally observed in areas where their sounds were recorded, indicates a value of underwater listening in studying the distributions, even limited ones, of some sound-producing species.

Listening equipment used in the investigation consisted of an AX-58-C Rochelle salt hydrophone and a Woods Hole Suitcase amplifier; an undesignated Rochelle

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TABLE I

Fishes making no sounds or only chewing sounds during the Bimini study

Family	Species	Comment
<i>Acanthyridae</i>	<i>Acanthus coerules</i>	1 specimen
<i>Antennariidae</i>	<i>Histrio histrio</i>	1 specimen
<i>Apogonidae</i>	<i>Apogon maculatus</i>	1 specimen
<i>Balistidae</i>	<i>Canthidermis sabaco</i>	Several individuals
<i>Belonidae</i>	<i>Strongylura marinus</i>	1 specimen
<i>Chaetodontidae</i>	<i>Chaetodon striatus</i>	1 specimen
	<i>Pomacanthus paru</i>	A 4" specimen
<i>Clupeidae</i>	<i>Jenkinsia lamprotaenia</i>	Large school and individual specimens
<i>Echeneididae</i>	<i>Phtheichthys lineatus</i>	2 specimens
<i>Fierasferidae</i>	<i>Carapus affinis</i>	1 specimen
<i>Gerridae</i>	Unidentified majarra	Several specimens
<i>Gobiidae</i>	<i>Bathygobius soporator</i>	Feeding sounds recorded from a group. Male known to call in the breeding season (Tavolga, 1956).
<i>Haemulidae</i>	<i>Haemulon album</i>	Several specimens
	<i>Haemulon parra</i>	Several specimens
<i>Labridae</i>	<i>Halichoeres radiatus</i>	Feeding sounds recorded
<i>Lutianidae</i>	<i>Lutianus griseus</i>	1 specimen
<i>Malacanthidae</i>	<i>Malacanthus plumeri</i>	1 specimen
<i>Mullidae</i>	<i>Upeneus maculatus</i>	Feeding sounds recorded
<i>Ogocephalidae</i>	<i>Ogocephalus radiatus</i>	1 specimen
	<i>Ogocephalus vespertilio</i>	1 specimen
<i>Orectolobidae</i>	<i>Ginglymostoma cirratum</i>	1 specimen
<i>Pristidae</i>	<i>Pristis pectinatus</i>	1 specimen
<i>Rachycentridae</i>	<i>Rachycentron canadus</i>	1 specimen
<i>Scorpaenidae</i>	<i>Scorpaena plumeri</i>	1 specimen
<i>Serranidae</i>	<i>Promicrops itaiara</i>	1 specimen
<i>Sparidae</i>	<i>Calamus providens</i>	1 specimen
<i>Sphyraenidae</i>	<i>Sphyraena barracuda</i>	1 specimen

salt hydrophone and a modified Heathkit amplifier Model A-7C, or an Ekotape microphone Model 205. Recordings were made at $7\frac{1}{2}$ and $3\frac{3}{4}$ in./sec. on the Ekotape tape recorder and selected recordings have been analyzed on a vibration frequency analyzer, the Kay Vibralyzer. Sound-generating equipment used during the investigation consisted of a Hewlett-Packard audio oscillator Model LAJ or the Ekotape tape recorder, a Craftsman C550 amplifier, and a QBG transducer. All observations at sea were made in calm weather from the 30-foot motor launch RESEARCH of the Lerner Marine Laboratory, between 0800 and 1400 hours from 9 July to 12 August. Suitcase amplifier settings varied from 0 + 14 - 20 to 0 + 10 - 5. During work at sea, the hydrophone was suspended just above the bottom, or so that it cleared the bottom in the shoalest water in the listening area at drift stations.

Forty species of fishes, distributed among 29 families, were studied at Bimini

(Tables I and II). The stimuli used in eliciting sound in the laboratory were those of handling, capture in a net or feeding, or a combination of these. All sounds reported were recorded from isolated, submerged specimens, except the pectoral fin drumming and tooth stridulation of individual triggerfishes (Balistidae) which were not heard while the fish were being handled under water. All other sounds described were produced in air as well as under water, except the snap of the demoiselle, *Pomacentrus leucosticus* (Mueller and Troschel), which was recorded only from submerged specimens.

The species which produced no detectable sounds other than those of chewing

TABLE II
Characteristics of fish sounds recorded at Bimini

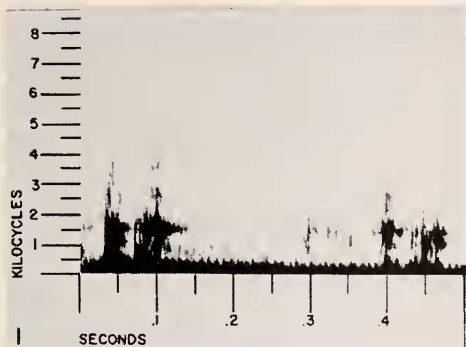
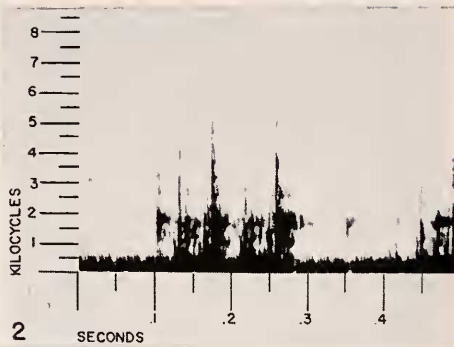
Family	Species	Vibration frequency analysis
<i>Balistidae</i>	<i>Balistes vetula</i> in air at microphone	Sound: Toothplate stridulation Duration: .12 sec./stridulation Frequency span: 0 to above 8 kc. Predominant intensities: .7-1.8 kc., 2.1-3.8 kc.
	<i>Melichthys piceus</i> in air at microphone	Sound: Toothplate stridulation Duration: .06 to .1 sec./stridulation Freq. span: 0 to above 8 kc. Pred. int.: 1.2 to 2.3 kc.
	<i>B. vetula</i> in air at microphone	Sound: Pectoral fin-drumming Duration: .03 sec./pulse Freq. span: 0 to 5.8 kc. Pred. int.: 1 to 1.7 kc.
	<i>M. piceus</i> in air at microphone	Sound: Pectoral fin-drumming Duration: .02 to .04 sec./pulse Freq. span: 0 to above 8 kc. Pred. int.: .7 to 2.2 kc.
	Feeding of a mixed group of the two spp. at AX-58-C hydrophone	Freq. span: 0 to above 8 kc. Pred. int.: .6 to 2.9 kc.
<i>Carangidae</i>	<i>Caranx hippos</i> hand-held in aquarium at hydrophone	Sound: Stridulation, pharyngeal teeth Duration: .06 sec./stridulation Freq. span: 0 to above 8 kc. Pred. int.: .3 to 1.2 kc., 1.7 to 3.3 kc.
<i>Chaetodontidae</i>	<i>Angelichthyes ciliaris</i> in cement tank at AX-58-C hydrophone	Sound: Grunt, single or repeated Duration: .06 to .1 sec./grunt Freq. span: 0 to 1.1 kc. Pred. int.: Below .5 kc.
	<i>Pomacanthus arcuatus</i> W. of Turtle Rocks at AX-58-C hydrophone	Sound: Grunt or moan-like sound Duration: .04 to .2 sec. Freq. span: 0 to 1.5 kc. Pred. int.: Below .5 kc.

TABLE II—*Continued*

Family	Species	Vibration frequency analysis
<i>Diodontidae</i>	<i>Diodon hystrix</i> hand-held in aquarium at hydrophone	Sound: Toothplate stridulation Duration: .09 sec./stridulation Freq. span: 0 to 8 kc. Pred. int.: 2.5 to 5.5 kc., with narrow intensity bands at 3, 4.3 and 5 kc.
<i>Haemulidae</i>	<i>Haemulon sciurus</i> hand-held in aquarium at hydrophone	Sound: Stridulation, pharyngeal teeth Duration: .02 to .1 sec./stridulation Freq. span: 0 to above 8 kc. Pred. int.: 1.5 to 4 kc.
<i>Holocentridae</i>	<i>Holocentrus ascensionis</i> in aquarium (Fig. 10) and at Turtle Rocks (Fig. 12); AX-58-C hydrophone	Sound: Thump-like single, or volleyed Duration: .04 to .1 sec./thump Freq. span: 0 to above 4 kc. Pred. int.: Below 1 kc.
<i>Pomacentridae</i>	<i>Pomacentrus leucostictus</i> in aquarium; male pursuing others of species at hydrophone	Sound: Single or repeated snaps Duration: .02 sec./snap Freq. span: 0 to 1.5 kc. Pred. int.: 0 to .8 kc.
<i>Serranidae</i>	<i>Epinephalus adsencionis</i> in cement tank at AX-58-C hydrophone	Sound: Vibrant grunt, single or repeated Duration: .04 to .1 sec./grunt Freq. span: 0 to .9 kc. Pred. int.: 0 to .3 kc.
	<i>Epinephalus striatus</i> in live car at AX-58-C hydrophone	Sound: Vibrant grunt, single or repeated Duration: .1 to .2 sec./grunt Freq. span: 0 to 2 kc. Pred. int.: 0 to .4 kc.
<i>Tetradontidae</i>	<i>Spheroides spengleri</i> hand-held in aquarium at hydrophone	Sound: Toothplate stridulation Duration: .07 sec./stridulation Freq. span: 0 to above 8 kc. Pred. int.: 1.3 to 3 kc.

are shown in Table I. Twelve species producing other-than-chewing sounds are listed in Table II, together with data derived from vibration frequency analysis. Of this latter group, only three species were identified as sources of sounds recorded during listening at sea—squirrelfish, Nassau grouper and black angelfish, *Pomacanthus arcuatus* (Linnaeus), all of which use the air bladder in sound production.

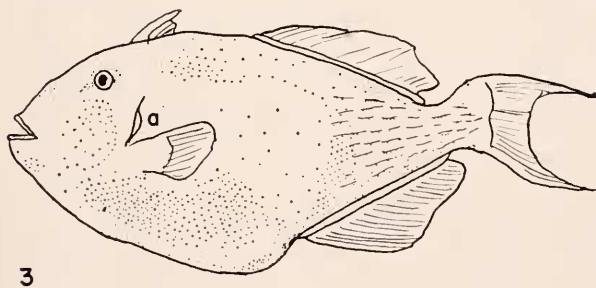
No individual free fishes were identified at sea as sources of stridulatory noises. Vibration frequency analysis of these latter sounds from recordings made at sea is rendered somewhat difficult by a broad band of sound with predominant intensities between 2 and 6 kc., which is characteristic of warmer seas, and which has generally been ascribed to snapping shrimp. It is not unlikely, however, that sounds created by the teeth of reef fishes (Table II—feeding of balistids) may contribute to this sound band, which on vibration frequency analysis tends to obscure upper frequency ranges of various sounds clearly discernible below the 2-kc level.

FIGURE 1. The pectoral fin-drum of *Balistes vetula* in air.FIGURE 2. The pectoral fin-drum of *Melichthys piceus* in air.

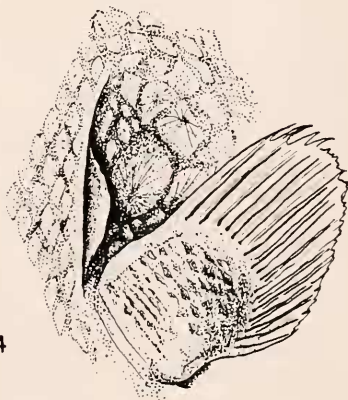
SOUND PRODUCTION AND BEHAVIOR OF BIMINI FISHES

In the following account, each family of which sound-producing representatives were studied at Bimini, is dealt with from the points of view of the sounds produced and the correlated behavior. Initial references are to earlier descriptions dealing with sound production in the families concerned.

Balistidae (Bridge, 1910, pp. 357, 361; Fish, 1948, pp. 15–19, 1954, pp. 62–65; Schultz and Stern, 1948, p. 132). The queen triggerfish, *Balistes vetula* L., and the black triggerfish, *Melichthys piceus* (Poey), each possesses above the base of the pectoral fin a thin membrane lying lateral to the air bladder and covered by scales larger and more plate-like than those elsewhere on the body (Figs. 3, 4), a characteristic of these genera of the *Balistidae* (Evermann and Marsh, 1900). Males and females removed from the water and handled, frequently elevated and rapidly fluttered the pectoral fins against this region, as described by Schultz and Stern (1948), resulting in the production of a throbbing sound (Table II; Figs. 1, 2). Bridge (1910, p. 357) attributes a throbbing sound primarily to movements of the pectoral girdle.



3



4

FIGURE 3. Outline of *M. piceus* showing (a) position of drumming membrane posterior to the gill opening. $\times 3$.FIGURE 4. Detail of the drumming membrane of *M. piceus*. $\times 2.5$.

Differentiation of the "drumming membrane" is not apparent externally in the ocean triggerfish (*Canthidermis sabaco* Poey), nor does this species during handling move the pectoral fins to the drumming position. Similarly, the toothplate stridulation readily demonstrated by the queen and black triggerfishes (Table II; Figs. 5, 6) during handling out of water was not performed by the several ocean triggerfish studied.

While tooth stridulation and pectoral fin drumming were not heard from isolated triggerfishes handled underwater, recordings made during the feeding about the hydrophone of a captive population of queen and black triggerfishes showed predominant intensities of accompanying sounds between .6 and 2.9 kc. (Table II), which essentially spans the frequency ranges of predominant intensities obtained during tooth stridulation by these species in air. It was not possible to ascribe any specific sounds recorded at sea to triggerfishes, although their feeding activity probably contributed to background sounds recorded. They are common in the area studied.

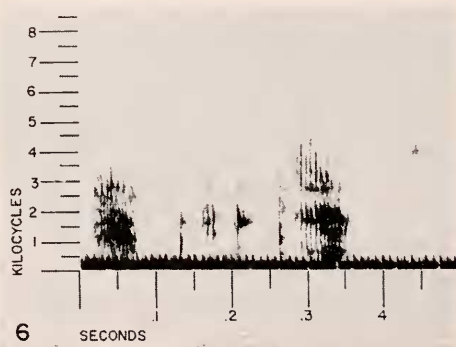
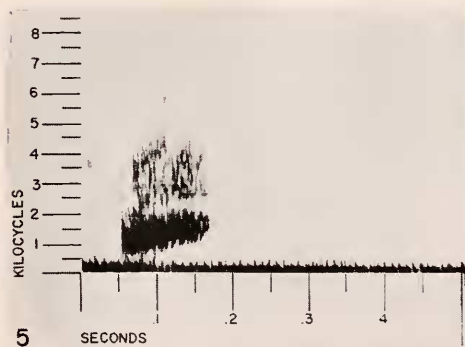


FIGURE 5. Tooth stridulation of *B. vetula* in air.

FIGURE 6. Tooth stridulation of *M. piceus* in air.

Carangidae (Bridge, 1910, p. 363; Fish, 1948, pp. 25-30). The pharyngeal tooth stridulation of *Caranx hippos* (Linnaeus) was recorded in a laboratory aquarium during handling of a 3.5-inch individual (Table II; Fig. 7). The sound recorded was not identified in any recording made at sea. Similar sound production in a related species, *Caranx crysos* (Mitchill), has been described by Fish (1954), but the thump she describes as occurring during shock was not heard during handling of the small specimen, nor was any detectable sound recorded from adult carangids swimming around and past the hydrophone at sea. A local fisherman related the stridulatory sound to "rattling of the ear bones" and asserted that a hooked specimen making this noise attracts other individuals of the species.

Chaetodontidae (Bridge, 1910, p. 361). The vibrant deep grunts of the queen, *Angelicthyes ciliaris* (Linnaeus), and black, *Pomacanthus arcuatus* (L.), angelfishes (Table II) are not easily distinguished from those of the serranids with which they may occur. Vibration frequency analysis shows (Fig. 8) a tendency for highest frequencies of the angelfish grunts to be located in the middle of the call, whereas serranid grunts tend to be initiated with high frequency spikes. Each

may vary in the direction of the other, however, and since serranids and angelfishes tend to occur in similar areas, the sounds of the two may be confused. Field and laboratory observations indicated that serranids are far more prolific in call production under ordinary circumstances than are the angelfishes.

Under laboratory conditions, both queen and black angelfishes produce the grunt during feeding on bits of conch, and when startled to quickened swimming by an observer. The deeply recessed air bladder, as seen in the black angelfish, bears no intrinsic muscles, and sound production is due to the contraction of axial musculature adjacent to the air bladder. Each quick motion of a black angelfish nibbling at the hydrophone at sea resulted in a brief grunt, although more leisurely swimming of both species in laboratory tanks was not accompanied by sound production. Handling of black angelfish under water brings forth brief grunts of low intensity, coinciding with body muscle contractions. Uniquely among species studied, the black angelfish, usually in pairs, readily approached and butted against the hydrophone at sea.

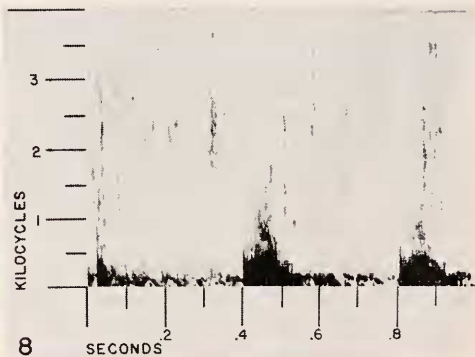
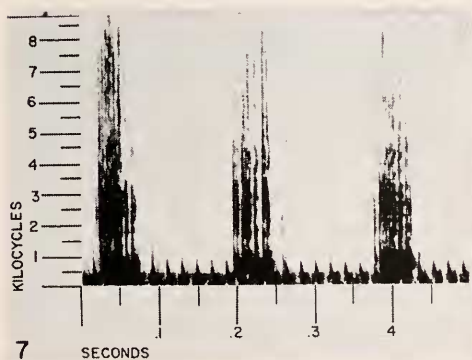
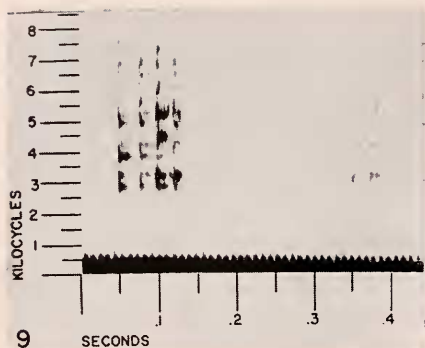
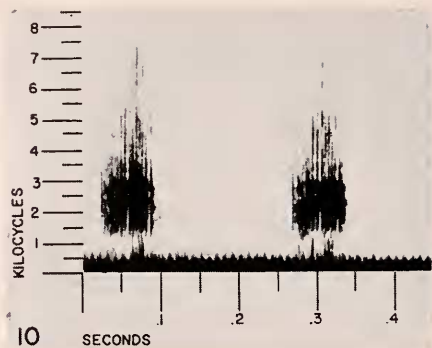


FIGURE 7. Pharyngeal tooth-stridulation of *Caranx hippos* in aquarium.

FIGURE 8. A short and two longer calls of *Pomacanthus arcuatus* west of Turtle Rocks, the latter during approach of another *P. arcuatus*. Snapping shrimp in background.

The deeply recessed position of the air bladder brings it into intimate association with surrounding peritoneum, and to the latter attach many of the axial muscle fibers heavily surrounding the slender ribs. These attached fibers appear to maintain a tension on the wall of the air bladder; cutting of the fibers creates a resonance within the bladder, and results in its partial collapse.

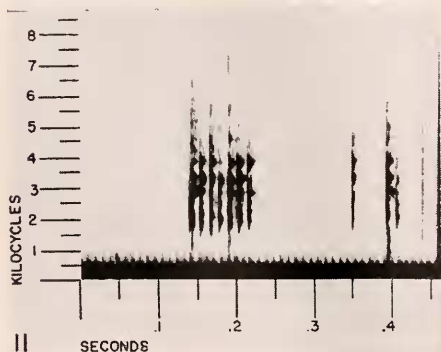
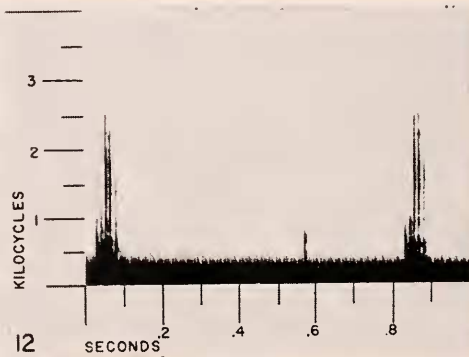
The maximum duration of angelfish grunts obtained during this investigation occurred west of Turtle Rocks on 10 July (Fig. 8), when an adult black angelfish examining the hydrophone and butting gently at its rubber case suddenly gave vent to prolonged, rather moan-like sounds, each of .2-sec. duration, and swam toward an approaching fish of the same species. The two fish faced each other for a few moments, after which both came quietly to the hydrophone and finally swam off together. The interpretation of a recognition signal in the prolonged grunts was rather difficult to avoid, for prior to production of the longer grunts, the first fish produced shorter, sharper sounds during its examination of the hydrophone. On another occasion, 12 July in the same area, sounds similar to the shorter grunts

FIGURE 9. Toothplate stridulation of *Diodon hystrix* in aquarium.FIGURE 10. Toothplate stridulation of *Spheroides spengleri* in aquarium.

were recorded as a pair of black angelfishes butted several times against a pair of cowfish, *Lactophrys tricornis* (L.), approximately 6 feet from the hydrophone.

No sounds were recorded from the single species of butterflyfish studied, *Chaetodon striatus* L., nor were sounds recorded from an immature specimen (4-inch, total length) of the French angelfish, *Pomacanthus paru* (Bloch).

Diodontidae, *Tetrodontidae* (Fish, 1948, 1954; Burkenroad, 1931). The porcupinefish, *Diodon hystrix* L., and the puffer, *Spheroides spengleri* (Bloch), were so similar in acoustical behavior as to merit a single discussion (Table II). Both produce sound during and after inflation by stridulation of the toothplates, the sound being of a klaxon-like variety (Figs. 9, 10). Only feeding sounds were recorded from undisturbed individuals. Frequencies of greatest intensities are similar in chewing and stridulation noises, although these levels vary between the two species (Table II) and may be expected to vary with size. Only a single individual of each was recorded at Bimini. Observations on these species and on the common puffer, *Spheroides maculatus* (Bloch and Schneider) of the Woods Hole area suggest that the stridulatory sound is more readily elicited from smaller individuals than from full-grown animals.

FIGURE 11. Pharyngeal tooth stridulation of *Haemulon sciurus* in aquarium.FIGURE 12. Single thump-like sounds of *Holocentrus ascensionis* in cement tank.

Haemulidae (Burkenroad, 1930, 1931; Fish, 1948, pp. 63–66; Schultz and Stern, 1948, p. 131). Although the fishes called grunts are notoriously noisy species of warmer marine waters, due to the rasping stridulation of the pharyngeal teeth, observations at Bimini indicated that not all species of the *Haemulidae* are equally important sound producers (Tables I and II). The haemulid rasp was not identified in any recordings made at sea; it was heard only from hand-held specimens of the blue-striped (Table II; Fig. 11) and yellow grunts, *Haemulon sciurus* (Shaw) and *H. flavolineatum* (Desmarest), respectively; no recordings

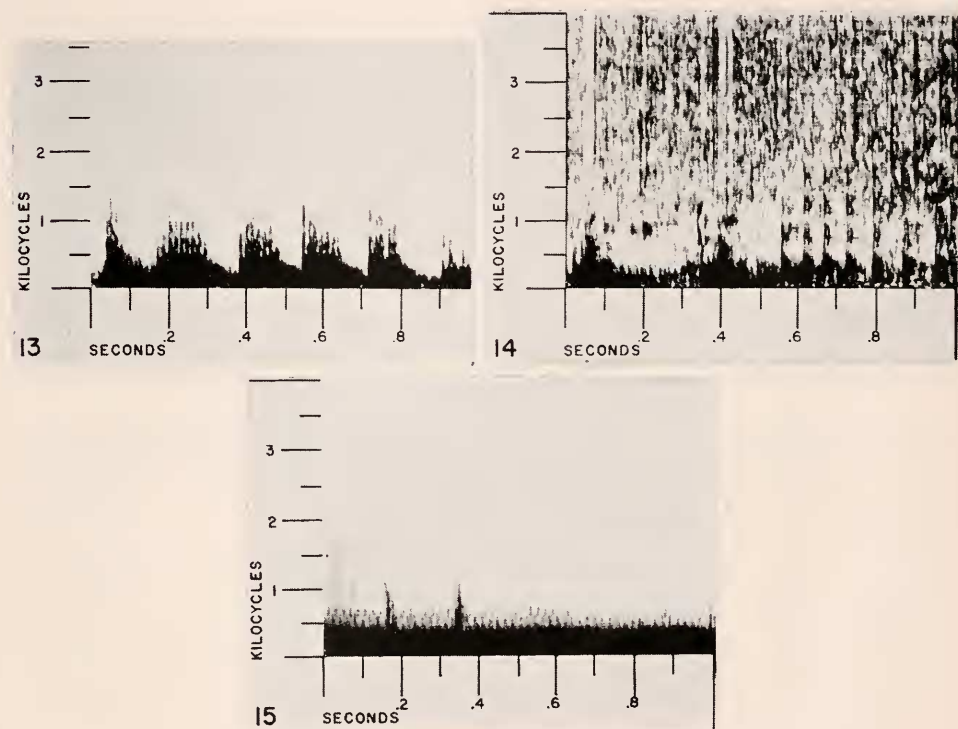


FIGURE 13. Grunts of *Epinephalus striatus* in cement tank.

FIGURE 14. Two *E. striatus* grunts (left) and a volley of thump-like sounds of *H. ascensionis* west of Turtle Rocks. Snapping shrimp in background.

FIGURE 15. Snaps of male *Pomacentrus leucostictus* in aquarium.

of the latter were obtained. The observations of Burkenroad (1930) which related the sounds of *Haemulon* to movements of the pharyngeal teeth were confirmed, with the exception that the association between the dorsal pharyngeal teeth and the anterior end of the air bladder seems more important in resonating the rasping sound than does the varying relation between the air bladder and the lower pharyngeal teeth. The opercula are somewhat extended during sound production. Rubbing together of dissected pharyngeal toothplates produces a much fainter sound than that produced by the living fish.

Holocentridae (Fish, 1948). Sound production by the squirrelfish, *Holo-*

centrus ascensionis, said to have derived its name from its chattering call (D. de Sylva, personal communication), is characteristic of the western edge of the Great Bahama Bank (Table II; Fig. 12, 14). It was recorded only along, and mainly to the west of, the island and rock chain extending from North Bimini south to South Cat Cay (Tables III and IV; Fig. 16). In rocky areas of the bottom along a relatively narrow area probably extending not far below the limits of visibility from the surface, squirrelfish are characteristically found in the daytime each hovering near a depression approximately large enough to receive a single fish. Generally living in higher parts of ledges than the grouper, an occasional squirrelfish inhabits a rocky fissure with *E. striatus*. Collection of squirrelfish in traps up to

TABLE III
Grouper and squirrelfish sound production along the western edge of the Great Bahama Bank in the Bimini area

Recording station	Duration of recording	Calls/minute		
		Grouper	Squirrelfish	Both
1) At 15 fa. depth W of Moselle Shoal, drifting N	13 min.	.08	0	.08
2) At 25 fa. depth SW of (1), drifting N	18 min.	.4	0	.4
3) W of gap between Round and Turtle Rocks	6 min.	1.0	5.2	6.2
4) W of Turtle Rocks	5 min.	.2	7.2	7.4
5) W of Turtle Rocks	11.5 min.	.8	6.3	7.1
6) W of Turtle Rocks	45 min.	1.9	9.5	11.4
7) W of Turtle Rocks, drifting SE	14 min.	.6	3.4	4.0
8) W of Triangle Rocks, drifting NE	10 min.	1.3	3.3	4.6
9) West of Triangle Rocks	13 min.	1.7	3.2	4.9
10) W of gap between Piquet and Triangle Rocks	15 min.	2.5	8.6	11.1
11) W of Piquet Rocks	12 min.	2.4	4.1	6.5

Average number of calls/minute (11 stations):

Grouper	1.2
Squirrelfish	4.6
Both	5.8

a mile east of Turtle Rocks and occasional sightings in deeper reaches east of the Bimini-Cat Cay chain indicated that the species may move beyond its more common daytime habitat along the outer face of the Bank. Holocentrids are mainly nocturnal in their habits (Barbour, 1905, p.119; Randall, 1955, pp. 33, 38) and at night their local distribution may be considerably more dispersed than during the daytime, although the species considered here is said to return to the same hole each day (Ray and Ciampi, 1956, p. 207).

Squirrelfish sounds are produced by contractions of body wall musculature against the rather firm-walled air bladder which is closely associated with the rib cage. The first three ribs are expanded, flattened and thinned dorsally, and are intimately associated with the air bladder wall; more posterior ribs are easily

separated from the bladder. Physiological stimulation indicated that the musculature chiefly responsible for sound production was that attaching to the dorsal portions of the first three ribs, which appear to serve as drumheads. The structure of the air bladder, and its close relationship with the auditory region of the skull, have been described by Nelson (1955).

The thump-like sounds of squirrelfish may be repeated singly at irregular intervals or produced in rapid volleys; they are more sharply peaked on vibration frequency analysis than are the sounds of angelfish and grouper. When produced by

TABLE IV

Grouper and squirrelfish sound production over the Great Bahama Bank in the Bimini Area

Recording station	Duration of recording	Calls/minute		
		Grouper	Squirrelfish	Both
1) On Moselle Shoal	23 min.	.04	.06	.1
2) Over wreck ENE of North Rock	27 min.	.4	0	.4
3) At North Rock, E side	27.5 min.	.04	.2	.2
4) At Crossing Rocks, W side	37.5 min.	.1	1.0	1.1
5) In Bimini Harbor entrance, drift to N	6.5 min.	0	.6	.6
6) 50' off S. Bimini, W side	13 min.	.7	.2	.9
7) At Round Rock, W side	8 min.	1.0	0	1.0
8) At Round Rock, E side	9 min.	.3	0	.3
9) On line between Turtle and Round Rocks, drift NW	10 min.	.9	1.9	2.8
10) Same station	30 min.	1.4	1.8	3.2
11) North end of Turtle Rocks, E side	4 min.	0	0	0
12) Same station	3 min.	0	0	0
13) On line between Triangle and Turtle Rocks, drift NE	12 min.	.4	2.2	2.6
14) Concrete shipwreck, E of Turtle Rocks	9 min.	0	0	0
15) Triangle Rocks, E side	11 min.	0	.6	.6
16) Dollar Harbor	5.5 min.	0	0	0
17) Wedge Rocks, NE side	8 min.	.8	1.4	2.2

Average number of calls/minute (17 stations):

Grouper	.3
Squirrelfish	.5
Both	.8

startled or handled squirrelfish, the sounds are volleyed in bursts of 4 to 20. Singly-produced sounds are of longer duration than those produced in volleys; these singly-produced sounds are not dissimilar to the ear from the sounds of Nassau grouper, although they cover a greater frequency span than do those of the grouper when both are recorded at the hydrophone.

Undisturbed squirrelfish confined in laboratory aquaria and outdoor tanks remained silent during listening periods of up to three hours; confined specimens produced sounds only when handled, fed or startled. Quickened swimming during feeding was characterized by sound production of a considerably lower intensity

than that produced during handling of the fish. Sudden startling of confined squirrelfish generally resulted in volleys of sound production.

At sea, squirrelfish were sometimes heard when no individuals were sighted, but the acoustical behavior of the species was characteristic when specimens were approached by the suspended hydrophone at drift stations. This behavior included

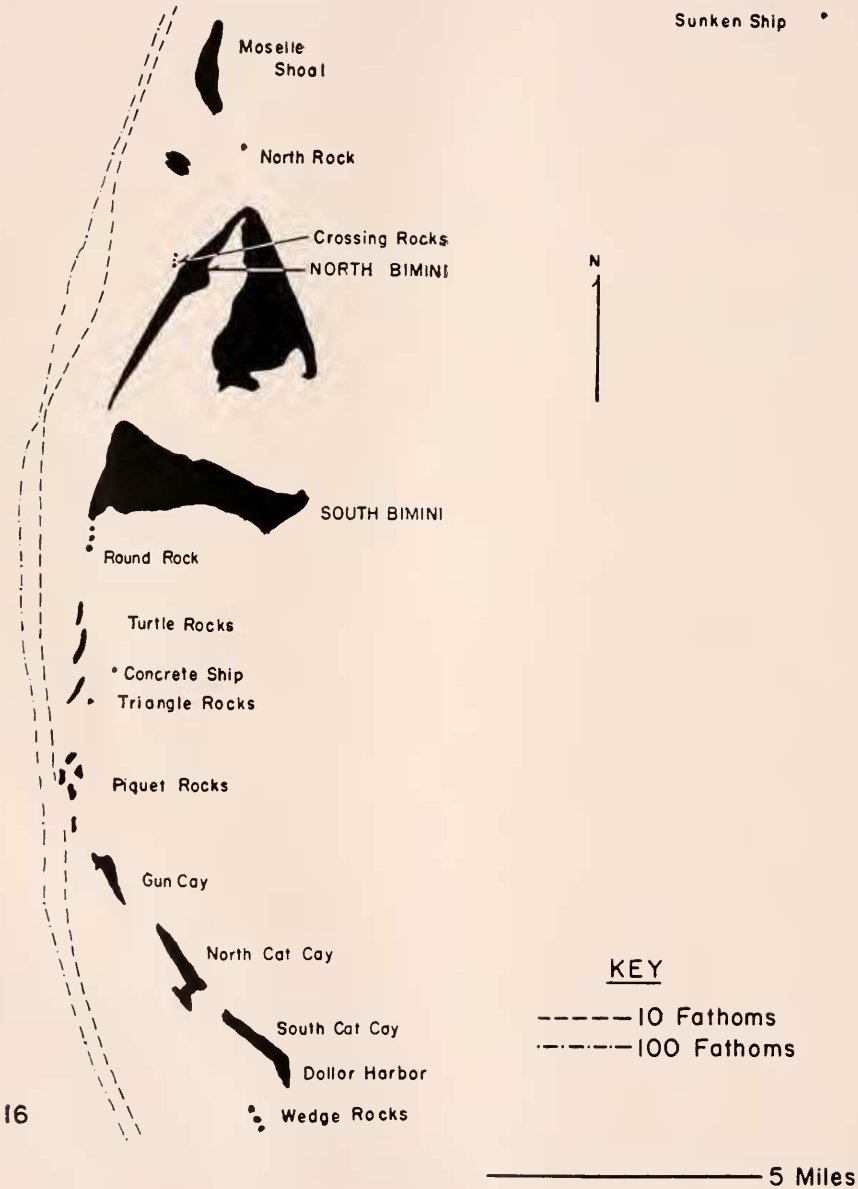


FIGURE 16. The Bimini area from Moselle Shoal to South Cat Cay.

erection of the spiny fins, adjustment of position so that an eye was directed toward the approaching hydrophone, movement toward a rocky depression near which the fish hovered, and production of the call in volleys of 3 to 20 individual pulses. The continuing approach of the hydrophone resulted in the fish's moving into its rocky shelter.

Pomacentridae (Fish, 1948, pp. 59-63). The sharp but rather faint knocks or snaps produced probably only by males of the demoiselle, *Pomacentrus leucostictus* (Mueller and Troschel), were recorded when a given individual suddenly dashed from cover to pursue other individuals approaching its place of concealment (Table II; Fig. 15). These were heard on several occasions. The behavior was similar to that of a sciaenid, *Corvina nigra* (Bloch) described by Dijkgraaf from Naples (1947).

Serranidae (Fish, 1954, pp. 36-44). The air bladder of the Nassau grouper, *Epinephalus striatus*, is thin-walled and lacks intrinsic muscles, yet this species equals the squirrelfish in its importance as a source of marine sound in the Bimini area (Table II; Figs. 13, 14). Contractions of body wall musculature appear to be responsible for the sound production, while the unusually heavy peritoneum stretched over the air bladder and adjacent organs apparently acts as the sounding board. Appropriate stimulation of opened fishes brought about some sound production, even after deflation of the air bladder. The strong contractions of body wall musculature accompanying production of the call are visible externally, and are easily elicited by startling or handling the fish in laboratory tanks. Sounds similar to those produced on alarm, but of a somewhat lower intensity, are produced during quickened swimming accompanying feeding.

Like the squirrelfish, the Nassau grouper inhabits the underwater ledges west of the Bimini-Cat Cay chain of rocks and island (Fig. 16). Its distribution is broader from east to west than that of the squirrelfish, since it was sighted where rocky fissures occurred in an otherwise sandy bottom in the Bimini lagoon, and it was seen and recorded in a shipwreck approximately 11 miles northeast of North Bimini Island on the Great Bahama Bank (Station 2, Table IV; Fig. 16). Unidentified sounds thought to originate from serranids were recorded at depths exceeding 15 fathoms west of North Bimini Island (Stations 1 and 2, Table III), from which depths serranids have been obtained at Bimini (Scholander *et al.*, 1951; Scholander and van Dam, 1954).

The Nassau grouper tends to be more secretive in its habits than the squirrelfish, ordinarily lying deeper in rocky fissures or well beneath overhanging ledges on the outer faces of which squirrelfish are more frequently seen. In acoustical behavior, the two are similar. As the suspended hydrophone approaches a grouper, the fins are erected and the fish retreats to cover, accompanying the retreat with the characteristic vibrant grunts. Like the call of the squirrelfish, that of the grouper was sometimes heard when no individual was sighted. The call is a characteristic marine sound of the area immediately west of the Bimini-Cat Cay chain.

The sound of the rock hind, *Epinephalus adscensionis* (Osbeck) (Table II), while of markedly lower intensity than that of the Nassau grouper, is produced under similar circumstances in laboratory tanks and is of similar characteristics. It was never specifically recognized during recording at sea. No sounds whatever were recorded from a captive *Promicrops itaiara* (Lichtenstein) weighing in the

neighborhood of 300 pounds, although the fish on one occasion very nearly swallowed the hydrophone.

DISTRIBUTION OF GROUPER AND SQUIRRELFISH SOUNDS IN THE BIMINI AREA

The distribution of squirrelfish and Nassau grouper in the Bimini area has been summarized above. Determination of this distribution was based on both visual and aural observations. The sounds of these species were selected to explore the possibility of determining the distribution of sonic species by aural means alone.

The total area of observation extended approximately 20 miles along the north-west edge of the Great Bahama Bank (Fig. 16), from Moselle Shoal on the north to Wedge Rocks on the south, and in an east-west direction from the location of a sunken freighter on the Great Bahama Bank ($25^{\circ} 49' N, 79^{\circ} 7' W$) 10.7 miles on a heading of 75 degrees from the northern tip of the Bimini Islands, to a station over an approximate depth of 150 feet southwest of Moselle Shoal. Recordings were made at 28 stations (Tables III and IV), all but two (Stations 1 and 2, Table III) being approximately on or within the 6-fathom line to permit observation of fishes during recording. Table III includes those stations, fixed and drift, at which recordings began on or were wholly confined to the edge of the Great Bahama Bank, to the west of the Bimini-Cat Cay chain; Table IV includes those stations located further in upon the Bank, in most cases immediately to the east of the Bimini-Cat Cay chain. The stations are in each case listed in order from north to south, and are referable to Chart No. 1854 of the United States Hydrographic Office, and to U. S. Coast and Geodetic Survey Chart No. 1112.

While not each call ascribed to either grouper or squirrelfish in Tables III and IV has been analyzed by vibration frequency analysis, a broad sample of recordings made at sea has been thus treated, and the results have indicated that the interpretations of recordings upon which Tables III and IV are based are correct. In erecting Tables III and IV, a rapid volley of either grouper or squirrelfish sounds has been characterized as a single call. Closely consecutive calls of the same species but of different individuals are usually interpretable as such on the basis of frequency differences, due to the origins' being at different distances from the hydrophone.

It will be noted in Table III that, although squirrelfish calls were lacking in the deepest stations recorded (1 and 2), along the sloping edge of the Bank they predominated over grouper calls by a factor of nearly 4. Moving of the listening station from the slope side of the Bimini-Cat Cay chain immediately to the Bank side (Table IV) resulted in an abrupt drop in incidence of calling by both species, but particularly by the squirrelfish. On the Bank itself, where squirrelfish were much less frequently sighted, their calls predominated over grouper calls by a factor of less than 2. The calling of these two species together was over 7 times as frequent along the edge of the Bank as to the east of its edge (Tables III and IV). The difference in incidence of calling between slope and Bank sides of the Bimini-Cat Cay chain is exemplified especially by comparison of Table III, Stations 4, 5 and 6, with Table IV, Stations 9, 10, 11 and 12. Short moves of the listening station resulted in marked differences in the incidence of underwater biological sounds.

Although not indicated by the data presented in Tables III and IV, observations at drift stations (Table III, Stations 7 and 8; Table IV, Stations 9 and 13) indicated that as the hydrophone moved over alternately sandy and rocky bottom, the incidence of calling rose markedly as the boat moved over underwater ledges and fell over the sandy stretches; the incidence of calling thus provided an indication as to the type of bottom beneath the boat, and correlated with sightings of grouper and squirrelfish.

OTHER UNDERWATER SOUNDS OF THE BIMINI AREA

Sounds most frequently heard during the underwater listening in the Bimini area, other than those described, are (1) the snapping and crackling characteristic of tropical seas, generally attributed to snapping shrimp, but actually indistinguishable by methods commonly employed from the sounds of some stomatopods (Johnson, *et al.*, 1947; Moulton, 1957); (2) a rattling sound like that produced by the spiny lobster, *Panulirus argus* (Moulton, 1957); and (3) another unidentified rattling sound with its predominant frequencies lying between .5 and 1.3 kc., each pulse being of .02 second duration, and repeated at intervals of approximately .12 second in volleys of varying length. In addition to these, a distinctive series of sounds was recorded twice the same day (12 July 1956 at Stations 6 and 9, Table IV). At Station 6, the sound was a buzz-like whine singly produced; at Station 9, the same sound was preceded by a number of sharp metallic raps and was followed by a number of brief chirps of somewhat lower frequency than the raps. The metallic raps were so similar to the sound of pounding on a steel hull that two observers, prone at the glass panels, concluded a vessel to be bearing down on the listening post. Since the listening boat was quiet except for water noise along the hull, and since no other boats were within view to the horizon, it is assumed that the sounds were of biological origin, but the source is unknown. They do not correspond with known cetacean sounds (Mr. William Schevill, personal communication).

DISCUSSION

The behavior of the Nassau grouper and squirrelfish in the Bimini area furnishes a marked exception to the generalization (Fish, 1954, p. 7) that fishes in the field are silenced by strange contacts. Both of these species were obviously stimulated to active sound production by approach of the boat and suspended hydrophone at drift stations over shallow waters. The spiny fin erection and movement toward concealment of these species upon approach of the hydrophone were strongly suggestive that the sounds described are related to self-protection, a probability further suggested by production of the same sounds during handling of these fishes. Although some fishes may use echo-location (Griffin, 1955), there is no evidence at present of its being involved in the cases under discussion. Circumstances surrounding production of grouper and squirrelfish calls, as observed at Bimini, were similar to those that surround production of sea robin grunts (Moulton, 1956b). While the grunts are readily produced during handling by most specimens of the sea robins common at Woods Hole, *Prionotus evolans* (L.) and *P. carolinus* (L.), the grunts are also produced by sea robins contained together in live cars and living on the bottom. Sea robin grunts are not, however,

so easily stimulated by startling as are the sounds of Nassau grouper and squirrelfish which readily produced sounds recorded at sea after periods of confinement of two weeks in laboratory aquaria.

The squirrelfish is the most significant producer of underwater sound among fishes in the Bimini area, and if the 20-mile extent of the Bank area studied may be considered typical of the whole, of the edges of the Great Bahama Bank generally. In view of this significance, Fish's (1948, p. 44) estimate of the sonic importance of the Holocentridae as "probably none" must be rejected. Since holocentrids are of wide distribution in tropical and sub-tropical waters, it seems probable that their sonic importance extends to other waters than those of the Bimini area.

The acoustical behavior of the angelfishes (Chaetodontidae) has not been hitherto adequately described, but there can be little doubt that the behavior of the single specimen recorded at Turtle Rocks on 10 July furnished evidence of a call accompanying recognition behavior in this species. The black angelfish which is most common of the angelfishes in the Bimini area, has a tendency to examine underwater objects (hydrophone, swimming cowfishes), such examination being accompanied by sounds of briefer duration than those proposed as a part of recognition behavior. The black angelfish is usually observed in pairs during July and August at Bimini. It seems likely that chaetodontids may contribute to underwater sound in other tropical and sub-tropical areas, although they are not discussed among sound-producing fishes of the Pacific by Fish (1948).

Further evidence of the tendency of captive fishes to become silent unless disturbed was provided by all species studied during the summer of 1956. The only species to produce sound spontaneously in laboratory aquaria during listening periods of up to three hours, other than those produced during feeding and being startled, was the small pomacentrid, *Pomacentrus leucostictus*, probably a male, as it pursued other individuals encroaching on its hiding place.

As is the case along the northeastern coast of the United States where the most significant fish producers of underwater sound which have been identified (sciaenids, triglids, and batrachoidids) are fishes using, rather than skeletal stridulatory mechanisms, muscles in close association with the air bladder (Tower, 1908; Fish, 1954; Moulton, 1956b), a holocentrid, a serranid and a chaetodontid are the most frequently calling fishes of the area immediately about the Bimini-Cat Cay chain. Of the former, however, both sea robins and toadfish produce sounds with muscles intrinsic to the air bladder, while all three of the most important calling fishes of the Bimini area use muscles extrinsic to the air bladder in producing their sounds.

The structural specializations and behavioral patterns of the sound producing species studied at Bimini have provided further striking evidence of the significance of sound in the biology of the species concerned, and the consistent incorporation of sound production into behavioral patterns observed in the clear water about Bimini (Nassau grouper, squirrelfish, angelfish) strengthens a conclusion that sound is of significance to the species concerned. Yet, as has repeatedly been affirmed, clear evidence of effectiveness of the sounds concerned in modifying the movements of fishes in nature is still lacking, although Tavalga (1956) has observed the females of a goby to demonstrate increased activity during sound production

by the male in breeding. The sounds of all calling species studied at Bimini are produced by both sexes, except for the snaps of *Pomacentrus leucostictus*.

Experiments of playing into the water artificial sounds and recordings of natural sounds such as those that have elsewhere modified fish behavior (Moulton, 1956a, 1956b; Tavalga, 1956) had no notable effect in the Bimini area. During all listening at sea in the Bimini area, all during daylight, sound production was prolific or rare, depending on the distribution of the species concerned and not on alternating periods of quiet and of sound production which seem to characterize production of the staccato call of sea robins at Woods Hole (Moulton, 1956b). Therefore, these experiments are not reported in detail. The Nassau grouper and squirrelfish were never observed in areas where their calls were not heard at Bimini.

The most characteristic component of background noise in the Bimini area is the "crackle" so characteristic of warmer seas, and which has generally been ascribed to snapping shrimp (Johnson *et al.*, 1947). By the analysis methods used, this noise in the Bimini area presents components cumulatively spanning the frequency range examined (up to 8 kc.). The invertebrates largely responsible are a common stomatopod (*Gonodactylus oerstedii*) and several kinds of snapping shrimps, including *Alpheus armatus* and *Synalpheus* spp. (Johnson *et al.*, 1947; Pearse, 1950; Moulton, 1957). The sound spectra obtained during this study from recordings of feeding and of stridulation sounds of various fishes indicate that in regions where producers of such sounds are numerous, they may contribute extensively to the spectrum of underwater sounds generally attributed to invertebrate sound producers.

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SUMMARY

1. On the basis of observations and recordings at sea and in the laboratory, the acoustical behavior of 13 species of Bahamian fishes is described, and their sounds are defined. Twenty-six species producing no calls in the course of this study are specified.

2. The most important sound-producers among fishes of the Bimini area are the squirrelfish, *Holocentrus ascensionis*, and the Nassau grouper, *Epinephalus striatus*. Their characteristic sounds may be anticipated when these species encounter a strange object at sea, and probably generally during the daytime along the edges of the Great Bahama Bank.

3. A single observation has indicated that calling is a component of recognition behavior in the black angelfish, *Pomacanthus arcuatus*. The families Chaetodontidae and Holocentridae should be added to lists of fish families containing calling members.

4. The usefulness of underwater listening in studying the distribution of some calling fishes has been demonstrated in the cases of the squirrelfish and Nassau grouper.

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